Theoretical consequences of trait-based environmental filtering for the breadth and shape of the niche: new testable hypotheses generated by the Traitspace model

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Abstract

Every species on Earth fills a unique environmental niche that is driven, in part, by the process of environmental filtering, where the adaptive value of the functional traits of individuals determine their fitness within the given environmental conditions. Despite its long-standing importance in ecology, theoretical investigations of environmental filtering have lagged behind studies of species interactions and neutral dynamics. A new statistical model of trait-based environmental filtering can be a useful tool for exploring the logical consequences of this process while holding all other processes constant. The model uses the logic of objective Bayesian inference to compute the probabilities of species within different environments using two sources of information: the location and dispersion of species within functional trait space, and the statistical relationship between traits and environmental gradients. By varying key parameters in the model, we highlight several testable hypotheses for trait-based ecology. First, niche breadth decreases as intraspecific trait variation decreases, as the strength of the environmental filter increases, and if the trait values do not enhance fitness in any environmental condition in the landscape. Second, niche shape is determined by the form of the trait-environment relationships, where species with extreme trait values are predicted to dominate at the environmental extremes when traits are linearly related to the environment, species with intermediate trait values generally have a selective advantage across a broader environmental range, and bimodal species response curves can occur independently from negative species interactions. The generality of these modelling results can be tested using empirical data from any ecosystem.

Keywords: functional traits, habitat filtering, trait convergence, predictive model, community assembly, species distribution modelling

1. Introduction

Environmental filtering is one of several important processes structuring the composition of ecological communities along environmental gradients (Keddy, 1992; Ackerly, 2003), yet it has received less theoretical investigation than species interactions and neutral dynamics within communities (May, 1973; Tilman, 1982; Hubbell, 2001; Chase and Leibold, 2003). The consequences of changing key parameters in population-based models of species interactions (e.g. growth rate, interaction coefficients, rates of resource reduction), have led to several long-lasting principles in ecology, such as the competitive exclusion principle (Gause, 1934), limiting similarity (MacArthur and Levins, 1967), the effects of resource reduction on growth rates of competitors or mutualists (Tilman, 1982; Hoeksema and Bruna, 2000), and the storage effect (Chesson, 2000). There have been many strong empirical tests of coexistence theories (Miller et al., 2005), and there have been some recent theoretical explorations of environmental filtering (Shipley, 2010; Maire et al., 2013), but broadly speaking, the literature on species coexistence within communities has been dominated by theory development, whereas the literature on environmental filtering across communities has been dominated by empirical research. The consequence of this is that there are far more general principles and theories about species interactions within communities than there are about how species are sorted along environmental gradients. In short, we lack a robust quantitative theory of environmental filtering. Obtaining deeper insight into trait-based environmental filtering using a mathematical model would both advance a general understanding of the process and would help to provide a robust framework for interpreting subsequent empirical results.

Every species on the planet fills a unique environmental niche (Gleason, 1926; Austin, 1985) that is driven, in part, by the process of environmental filtering where species are sorted by their physiological adaptations (Keddy, 1992; Ackerly, 2003). Predicting the outcome of this filtering process is critically important as rapid environmental changes are driving geographical range shifts across multiple taxa (Chen et al., 2011), but we still lack the ability to translate the functional traits of a species into a reliable prediction of its distribution in space and time, which has been a long-standing goal in ecology (Lavorel and Garnier, 2002). Predicting species distributions using a variety of sophisticated algorithms has improved models of species distributions and forecasts of range shifts under global change (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). Species distribution models can use either correlative or mechanistic approaches, but both approaches have their strengths and weaknesses. Predicting the correct shape and extent of the environmental niche of any given species using information encoded their functional traits would represent a significant empirical advance (Kearney et al., 2010).

Environmental niche breadth describes the suite of environments or resources that a species can inhabit or use (Gaston et al., 1997; Slatyer et al., 2013). The environmental niche (hereafter, ‘niche’) can be described by its mean position and breadth along any set of environmental gradients (Schoener, 1989). Niche breadth is important because it is related to range size (Banta et al., 2012; Boulangeat et al., 2012; Slatyer et al., 2013) and range size is a strong predictor of extinction risk (Gaston and Fuller, 2009). Species with narrower niche breadths may lose more habitat in the future or be the least tolerant to climate change (Thuiller et al., 2005; Morin and Lechowicz, 2013). Understanding the drivers of niche breadth may lead to better predictions of which species are the most vulnerable to global change drivers. Intraspecific variation may play a large role in determining niche breadth because species that are genotypically more diverse or more plastic in their response to the environment may be more resilient to environmental change (Rehfeldt et al., 1999; Angert et al., 2011).

Trait-based environmental filtering

The shape of the niche (i.e. the form of the species response curve illustrated as changing relative abundances along an environmental gradient) has classically been modelled as a symmetric bell-shaped curve (Gauch and Whittaker, 1972). Fundamental niches may be unimodal bell-shaped curves, but realised niches likely vary from bell-shaped, to skewed, to markedly asymmetric bimodal curves due to the presence of a superior competitor or other interactions (Mueller-Dombois and Ellenberg, 1974). Empirical studies have shown that niches are often skewed and sometimes multimodal (Minchin, 1989; Austin et al., 1990), and competition is consistently invoked to explain departures from bell-shaped response curves. Here we investigate the theoretical shape of the niche in the absence of competition.

Many models of species interactions ignore but do not deny the importance of environmental filtering; likewise, models of environmental filtering ignore but do not deny species interactions (Shipley et al., 2006). Theoretical consequences of varying key parameters in models of species interactions within communities that do not implicitly incorporate environmental filtering across communities have led to important conceptual advances (Gause, 1934). Similarly, by holding species interactions and all other processes constant, we can explore the logical consequences of trait-based environmental filtering.

Two recent models have been proposed to explore trait-based environmental filtering. The CATS model obtains the most even predictions of species relative abundances subject to community-level mean trait constraints (Shipley et al., 2006). It requires observations (or predictions) or community-level mean trait values in order to predict species abundances and does not explicitly incorporate intraspecific trait variation. Alternatively,the ‘Traitspace’ model, uses objective Bayesian inference to compute species relative abundances by combining two sources of information: the location and dispersion of species within functional trait space, and the statistical relationship between traits and environmental gradients (Laughlin et al., 2012). This model does not require knowledge of the mean value of a trait in a community to predict species abundances and explicitly incorporates intraspecific trait variation. The similarities and differences between the two models has been discussed in detail elsewhere (Laughlin and Laughlin, 2013). The Traitspace model has been shown to make predictions of species distributions that closely match observations in the field (Laughlin et al., 2012; Laughlin et al., 2014), but the theoretical consequences of changing key parameters within this model have not been rigorously evaluated. Given that this model can accommodate any gradient, any species, and any quantitative trait, the model is broadly applicable to any ecosystem on the planet. Therefore, the objective of this study was to simulate hypothetical environmental gradients, traits, and species to determine how intraspecific trait variation and the strength and form of the environmental filter affect the predicted breadth and shape of the niche using the Traitspace model.

2. Material and methods

2.1. The Traitspace model: a mathematical translation of trait-based environmental filtering

The theory of environmental filtering proposes that functional traits dictate how species are sorted along environmental gradients (Keddy, 1992). Shipley (2010) refers to this process as ‘community assembly by trait selection’ and is the ecological consequence of natural selection (Shipley, 2010). The Traitspace model translates this proposition into a directed acyclic graph model: $\mathbf{E} \rightarrow \mathbf{T} \rightarrow \mathbf{S}$, where traits (**T**) mediate the relationship between species abundances (**S**) and environmental gradients (**E**) (Fig. 1). The fundamental difference between this approach and classic species distribution modelling (Elith and Leathwick, 2009) is the insertion of traits into the framework (Laughlin et al., 2012). The graph model is a simplification of a very complex process. It assumes that the feedback effect of species on the environment is negligible within the time frame of the study. Additionally, it does not take into account the effect of species interactions. However, these simplifying assumptions give us a framework with which to test whether the process of environmental filtering has had a significant effect on species composition. Within this framework, if we can quantitatively link species to trait values and link trait values to the environmental conditions, then we can estimate the probability (or relative abundance) of the i^{th} species in a given environment, i.e. $P(S_i|E)$. In this context, trait values that are more likely in a given environment are assumed to confer high adaptive value and will make individuals with these trait values more fit within a given environment. Therefore, ‘fitness’ in this context relates to species with trait values that have high likelihoods within the given environmental conditions.

The model merges two sources of information to obtain probabilities of each species given the environmental conditions (Laughlin et al., 2012). If one obtains (i) objective knowledge about the typical range of phenotypic traits within a species and (ii) objective knowledge about the adaptive value of traits for certain kinds of environments, then, we can use objective information about the environment of a site to derive the probability of a species occurring in that environment (Fig. 1).

To calibrate the model, one must first characterize the size and shape of the environmental filter by modelling traits as a function of the environment, i.e., $T = f(E)$ (Fig. 1). This can be done using regression models where environmental gradients are predictors and the traits are response variables. This calibrates the conditional distributions of traits given the environmental conditions $\varphi_{T|\mathrm{E}}$. Second, one must characterize the location and dispersion of each species in trait space using a probability density function (pdf) (Fig. 1). These pdfs can be simple multivariate Gaussians or more flexible mixture models (Fraley et al., 2012). This calibrates the conditional distributions of traits given species $\varphi_{T|\mathrm{S}i}$. Once the relationships between traits and environment are fitted, and once the trait distributions for each species in the species pool is known, then it is possible to estimate the likelihood of each species given an environment using Bayes theorem.

Deriving predictions of species relative abundances is accomplished in four steps. First, simulate community assembly stochastically by sampling a large number (e.g., N = 1000) of traits from the distributions $\varphi_{T|\mathrm{E}}$ at every value along the environmental gradients. Second, for every trait value sampled, compute the likelihood $P(T|S_i)$ of the given trait belonging to a particular species using the conditional distributions $\varphi_{T|S_i}$. Third, for every trait value sampled, compute the posterior distribution of species conditioned on both the trait data and the environmental conditions $P(S_i|T,E)$ using Bayes theorem:

$$P(S_i|T,E) = \frac{P(T|S_i)P(S_i)}{\sum_{i=1}^{S} P(T|S_i)P(S_i)}. \quad (1)$$

$P(S_i)$ denotes a flat (uniform) prior on the species. Note that Eq 1 is valid because we have $P(S_i|T,E) = P(S_i|T)$, which is an implication of the directed acyclic graph model. The choice of a uniform prior reflects that all species are assumed equally likely to occur prior to the analysis. This choice is important, since it implies that the posterior distribution is merely a normalized version of the likelihood. Thus, posterior probabilities of each species given the environment are obtained by objectively taking into account the likelihood of every trait value belonging to a particular species. The simulation step above ensures that only the trait values filtered by the environmental filter are considered. Alternative priors that reflect abundances in the landscape can be used to account for dispersal limitation (Shipley et al., 2012).

Lastly, integrate out the traits to obtain the relative abundances of species given the environmental conditions

$$P(S_i|E) = \int P(S_i|T,E)P(T|E)dT. \quad (2)$$

This integral often does not have a closed form solution, so by using Monte Carlo integration the desired conditional distribution is approximated as

$$P(S_i|E) \cong \frac{1}{N}\sum_{k=1}^{N} P(S_i|T_k,E)P(T_k|E). \quad (3)$$

Thus, the Traitspace model predicts the relative abundances of species given an environment by averaging out the effect due to traits. One could interpret these predictions as the relative abundances one would expect in a given environment ‘on average’. It is again important to note that these estimates are purely based on the calibrated trait environment relationship and the calibrated trait distributions for each species. These estimates do not take into account effects such as dispersal limitation or species interactions; they solely reflect the consequences of environmental filtering. An R script to implement the simulations is provided in Appendix 1.

2.2. Exploring the theoretical consequences of the model

The theoretical consequences of environmental filtering were explored by varying the following model parameters: (1) the number of environmental gradients (i.e. one or two), (2) the form of the trait-environment relationship (i.e., linear, nonlinear, flat), (3) the strength of the trait-environment relationship (i.e., the standard error of the linear model), (4) intraspecific trait variation, and (5) the number of traits (i.e. one or two).

Environmental gradients were simulated by generating evenly spaced values along a single gradient (centered on zero, ranging from -3 to 3), or by generating a grid of evenly spaced values along a two-dimensional surface (centered on the origin, with boundaries of -3 and 3 in both dimensions). Even spacing was used to ensure that there were adequate data points along the full breadth of the gradient and that visualizing the predicted species probabilities along the gradient was most straightforward.

The form and strength of the trait-environment relationship were varied by simulating trait values as functions of the environmental gradients. Traits were simulated as either linear (positive or negative), quadratic (peaked or u-shaped), or flat (no relationship) functions of the environmental gradients. When investigating niche breadth (described below), the strength of the relationship between traits and the environmental gradients were varied by varying the standard error of the linear model.

Species were simulated by spacing their trait distributions equally throughout either a one or two-dimensional trait space. This choice ensured that no species was functionally redundant. Intraspecific trait variance was varied by changing the standard deviations of the traits. For simplicity, the covariance between the two traits was fixed at zero.

We explored how changing model parameters influenced the predicted estimates of niche breadth and niche shape. The environmental niche can be defined as the range of environmental conditions in which the species occurs (Hortal et al., 2008). We defined niche breadth as the distance (along a one-dimensional environmental gradient) or area (within a two-dimensional environmental surface) within which a species attains a minimum 5% probability. We define niche shape as a discretized curve (or surface along two environmental gradients) obtained by plotting the predicted relative abundance of a species given environment $P(S_i|E)$, as a function of the environmental gradients.

The effects of intraspecific trait variation and the strength of the environmental filter on niche breadth were explored by comparing predicted niche breadth across all combinations of these factors. The effects of intraspecific trait variation were analyzed by setting the following standard deviations for each trait: 0.1, 0.5, 1, 1.5, and 2. The effects of the strength of the trait-environment relationship was analyzed also by setting the standard deviations for each relationship at the above levels. This analysis of niche breadth was constrained to the species that attained maximum probability in the middle of the environmental gradient, because the predicted response curve of this species was located entirely within the environmental gradient. Other species attained maximum probabilities at the ends of the gradient and so their niches were truncated, which would bias the estimation of their niche breadth.

3. Results

3.1. Niche breadth

Niche breadth decreases as intraspecific trait variation decreases and as the strength of the environmental filter increases (Fig. 2). These factors interact because the effect of intraspecific trait variation on niche breadth is muted if the relationship between traits and environmental gradients is weak: the slopes of the red lines (sd=0.1) that represent strong trait-environment relationships are steeper than the slopes of the purple lines (sd=2) (Fig. 2).

Niche breadth will be reduced to zero, i.e., the species will not occupy a niche, if their trait values are not likely within any environmental condition, i.e., the traits do not enhance fitness in any environmental condition (Fig. 3). This is detectable during the modelling process when the model-fitted trait values from the trait-environment regression model do not pass through the species locations within the trait space. With only one trait, all species will attain some level of probability, because an environmental gradient cannot “miss” a species, unless the species occupies a region of trait space that is far beyond the limits of the trait-environment relationship. However, consider the following examples where five species are distributed throughout an orthogonal 2-dimensional trait space (Fig. 3). The black lines or regions illustrated within these two-dimensional trait spaces illustrate the model-fitted mean trait values from the trait-environment regression models, and the Traitspace predictions following from these trait-environment regression models are illustrated immediately below the 2-dimensional trait spaces (Fig. 3). If the black lines or regions only overlap some species, then the other species will be selected against and will not occupy a niche (the blue and orange species in Fig. 3A and 3B are not predicted to occur substantially along the gradient). If the black lines or regions overlap more species in the trait space, then more species will occupy a niche along some part of the environmental gradient. In the case of a single environmental gradient, non-linear trait-environment relationships are necessary for all species to occupy an environmental niche (all five species are predicted to occur at some place along the gradient in Fig. 3C). In the case of two environmental gradients, there are generally far more possible ways to ‘travel’ through a 2-dimensional trait space, and therefore more species will occupy environmental niches (all five species are predicted to occur at some place along the gradient in Fig. 3D). When particular combinations of each trait-environment relationship yield model-fitted trait values that span a broad region throughout trait space, then more species occupy more environmental niches.

3.2. Niche shape

3.2.1. One trait and one environmental gradient - Species distributions that are governed by selection of a single trait as a linear function of a single environmental gradient will appear as symmetric, bell-shaped curves (Fig. 4A) because traits were simulated from the environmental filter which was modelled using a normal regression model. If the trait has no selective advantage along the gradient (i.e., the trait-environment relationship is flat and neutral), then the predicted species abundance distributions are the same across the gradient, but species with intermediate trait values tend to have larger predicted relative abundances than species with extreme trait values (Fig. 4B). If the trait is linearly related to the gradient, then species with extreme trait values dominate at the ends of the gradient whereas species with intermediate trait values will dominate in the middle of the gradient (Fig. 4C). If the trait exhibits a non-linear relationship to an environmental gradient, then bimodal species response curves can occur (Fig. 4D). If high values of a trait are selectively advantageous at intermediate locations along the environmental gradient, then species with low trait values are predicted to occur at either end of the gradient.

3.2.2. One trait and two environmental gradients - Adding multiple environmental gradients to the model changes species response curves into more complex multidimensional surfaces (Fig. 5). When viewed along a single dimension at a time, species distributions appear like response ‘envelopes’ rather than idealised curves (Fig. 5). If the trait has no selective advantage along either gradient, then the predicted species abundance distributions are the same across both gradients, but species with intermediate trait values tend to have larger predicted relative abundances than species with extreme trait values (Fig. 5B). If the trait is linearly related to both gradients, then species with extreme trait values dominate at the ends of the gradient whereas species with intermediate trait values will dominate in the middle of the gradient (Fig. 5C). If the trait is non-linearly related to the environmental gradient, then species with extreme trait values will dominate at intermediate locations along the gradient (Fig. 5D-E). In these cases, bimodal species response curves are predicted to occur.

3.2.3. Two traits - If no trait value exhibits a high likelihood along the environmental gradients, then the predicted species abundance distributions are the same across the gradients, but species with intermediate trait values have much larger predicted relative abundances than in the cases with just a single trait (Figs. 6B and 7B). If traits are linearly related to the gradient, then species with extreme trait values dominate at the ends of the gradient whereas species with intermediate trait values will dominate in the middle of the gradient (Figs. 6C-D and 7C-D). If both traits are non-linearly related to the environmental gradient, then species with extreme trait values will dominate at intermediate locations along that environmental gradient and bimodal species response curves are predicted to occur. However, the bimodal responses can be muted if one of the traits is linearly related to the environment (Fig. 6E-F and 7E-H).

4. Discussion

These modelling results have highlighted several theoretical consequences of trait-based environmental filtering that provide us with a set of testable hypotheses about the drivers of niche breadth and shape. First, niche breadth decreases as intraspecific trait variation decreases and as the strength of the environmental filter increases (Fig. 2), and when the trait values do not exhibit high likelihoods in any environmental condition (Fig. 3). Second, niche shape is determined by the form of the trait-environment relationships, where species with extreme trait values are predicted to dominate at the environmental extremes when traits are linearly related to the environment, species with intermediate trait values generally have a selective advantage across a broader environmental range, and bimodal species response curves can occur independently from negative species interactions (Figs. 4-7).

4.1. Consequences for niche breadth

Niche breadth decreases as intraspecific trait variation decreases. This trait-based model provides additional theoretical support for the importance of incorporating intraspecific trait variation into modelling frameworks for predicting community assembly and species responses to global change. Intraspecific variation is an ecologically important source of trait variation in plant communities (Albert et al., 2010; Messier et al., 2010) that can impact the outcome of community assembly (Jung et al., 2010; Violle et al., 2012; Jung et al., 2014). Species that are genotypically more diverse or more plastic in their response to the environment may be more resilient to environmental change (Rehfeldt et al., 1999; Angert et al., 2011). Species with broad niches tend to have larger range sizes and may lose proportionally less habitat under future climate scenarios than species with narrow niches (Thuiller et al., 2005; Morin and Lechowicz, 2013). If intraspecific trait variation can reliably predict niche breadth, then perhaps it can be used to prioritise species most at risk under global change scenarios.

Niche breadth decreases as the strength of the environmental filter increases. If the optimal trait value for enhancing fitness changes rapidly along an environmental gradient and if species differ in their trait values, then species turnover will be rapid and individual species will only be fit within a small range along the gradient. On the contrary, if the trait-environment relationship is weak, then a broader range of trait values will occur within any given environment. This can happen for two main reasons. First, the trait may not enhance fitness and performance at all and will therefore be irrelevant to community assembly, which is why it is important that we measure traits that have known impacts on ecological performance along environmental gradients. Second, a diversity of trait values may enhance species coexistence through niche complementarity, which would indicate that no single optimal trait value exists within an environment. These results confirm that quantifying the strength and sign of trait-environment relationships and determining which traits enhance fitness is prerequisite to improving our predictions of species distributions (Shipley, 2010).

Niche breadth decreases if the model-fitted trait values from the trait-environment regression models do not overlap species within trait space (Fig. 3). In other words, if a species does not possess the trait values that are likely to enhance fitness within a given environment, then that species will not be predicted to occupy any location along the environmental gradient. This result may help explain why some species are common and others are rare. Rare species may be rare because their trait values only enhance fitness within a narrow range of environmental conditions. Consistent relationships between traits and rarity have been difficult to detect (Murray et al., 2002), but perhaps trait-based explanations for rarity can only be made when traits are modelled as a function of local environmental conditions.

4.2. Consequences for niche shape

The form of the trait-environment relationship strongly dictates the shape of the niche, i.e. the shape of the species response curves (Austin, 1985). We tested the consequences of flat (i.e. neutral), linear, and nonlinear trait-environment relationships for the four combinations of either one or two traits and either one or two environmental gradients.

If the trait-environment relationship is flat, then species with intermediate trait values have the largest predicted abundances (Figs. 4-7). From the perspective of Bayesian probabilities, species with intermediate trait values are more probable along the entire range of a gradient when the trait-environment relationship is flat because for such species, both the $P(S_i|T_k,E)$ as well as the $P(T_k|E)$ will be larger resulting in higher posterior probabilities $P(S_i|E)$ using Eq. 3. Additionally, species with intermediate trait values are virtually always predicted to occupy some environmental niche space because the fitted trait values from the trait-environment relationships nearly always pass through the middle regions of trait space (Fig. 3). There are two possible explanations for this result. First, species with intermediate trait values may be generalists that can tolerate a broader range of environmental conditions. This hypothesis could be empirically tested by determining whether species that have intermediate trait values have higher average relative abundances and larger niche breadths than species that have extreme trait values. Alternatively, the result may be an artefact of assuming that trait values follow a normal distribution within each community. It is true that the assumed distribution will have an impact on the posterior probabilities (Eq 3). It is possible to assume a different distribution than normal (e.g. uniform) to model $P(T_k|E)$, but ideally the chosen distribution should be backed by empirical evidence. These distributional assumptions should be checked when applying the model with empirical data.

If the trait-environment relationship is linear, then species with extreme trait values are more likely to occur in extreme environmental conditions, suggesting that species with extreme trait values are specialists. Linear trait-environment relationships are commonly reported. For example, specific leaf area, height, and seed mass were on average highest at low elevation in the French Alps (de Bello et al., 2013). However, traits are likely to exhibit both linear and nonlinear relationships with different environmental conditions (de Bello et al., 2013). For example, the leaf economics spectrum may be positively correlated with soil fertility (Ordoñez et al., 2009), but may exhibit a peaked relationship with mean annual temperature, where low specific leaf area is selected in both extremely cold and hot environments (Laughlin et al., 2011).

Nonlinear trait-environment relationships yielded the most surprising results (Figs. 4-7). One of the most unanticipated results was that skewed and bimodal species response curves can theoretically be caused by environmental filtering alone. It has long been suggested that strong departures from bell-shaped curves, especially bimodal response curves, are due to the effects of species interactions (Mueller-Dombois and Ellenberg, 1974; Minchin, 1989; Austin et al., 1990). However, our results indicate that if traits are nonlinearly related to the environment, then niches can be bimodal. Nonlinear trait-environment relationships are common in empirical studies. For example, wood density can exhibit a u-shaped relationship with mean annual temperature because denser wood prevents both freeze and drought-induced cavitation, so high density wood is selectively advantageous in both extremely cold and hot environments (Laughlin et al., 2012). Why, then, do some species not occur in both semi-arid woodlands and subalpine forests if a single trait is advantageous in both environments? The reason is because multiple traits are selected by the environment, and if another trait is linearly related to the environmental gradient, then the bimodal response curve is muted.

5. Conclusions

Predicting species distributions continues to be a central goal in ecology (Guisan and Zimmermann, 2000; Austin et al., 2009; Elith and Leathwick, 2009), and forecasting species responses to global change is one of the most important challenges (Lavorel and Garnier, 2002; Thuiller et al., 2008; Guisan et al., 2013). Translating mechanistic processes, such as trait-based environmental filtering, into statistical models of species distributions provides a pathway for modelling species distributions as functions of ecophysiological tolerances (Kearney and Porter, 2009). Trait-based models in ecology are promising because predictions are based on generalizable properties of organisms, not simply taxonomic identification. Modelling the niche using functional traits (Kearney et al., 2010) to predict species and community-level responses to global change will be useful for developing sound restoration and management decisions (Laughlin, 2014).

By exploring the consequences of varying key parameters in a statistical model of trait-based environmental filtering, we have shown that functional traits can have important consequences on the shape and breadth of the niche. Intraspecific trait variation and the strength and form of the trait-environment relationship influence the predictions of species abundances and distributions. These modelling results provide a theoretical basis for a new set of hypotheses that can be tested empirically, and can also aid in the interpretation of existing empirical assessments of environmental niches. Patterns in nature that deviate from model predictions will inform us when other important ecological processes, such as species interactions and dispersal limitation, are operating. Applying this trait-based model will add rigour and generality to our forecasts of species range shifts in a rapidly changing world.

Classic theoretical models in ecology have tended to emphasize species interactions and neutral dynamics within communities over environmental filtering along environmental gradients (May, 1973; Tilman, 1982; Hubbell, 2001). The Traitspace model used here emphasizes environmental filtering over species interactions (Laughlin and Laughlin, 2013). We anticipate that the next generation models of community assembly will unify the mathematics of broad-scale environmental filtering and local-scale species interactions. Only then will our models be capable of making predictions of species abundances under both changing abiotic conditions and novel species interactions (Hobbs et al., 2009).

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Supplementary Material

Appendix 1. R script to run the Traitspace model of trait-based environmental filtering

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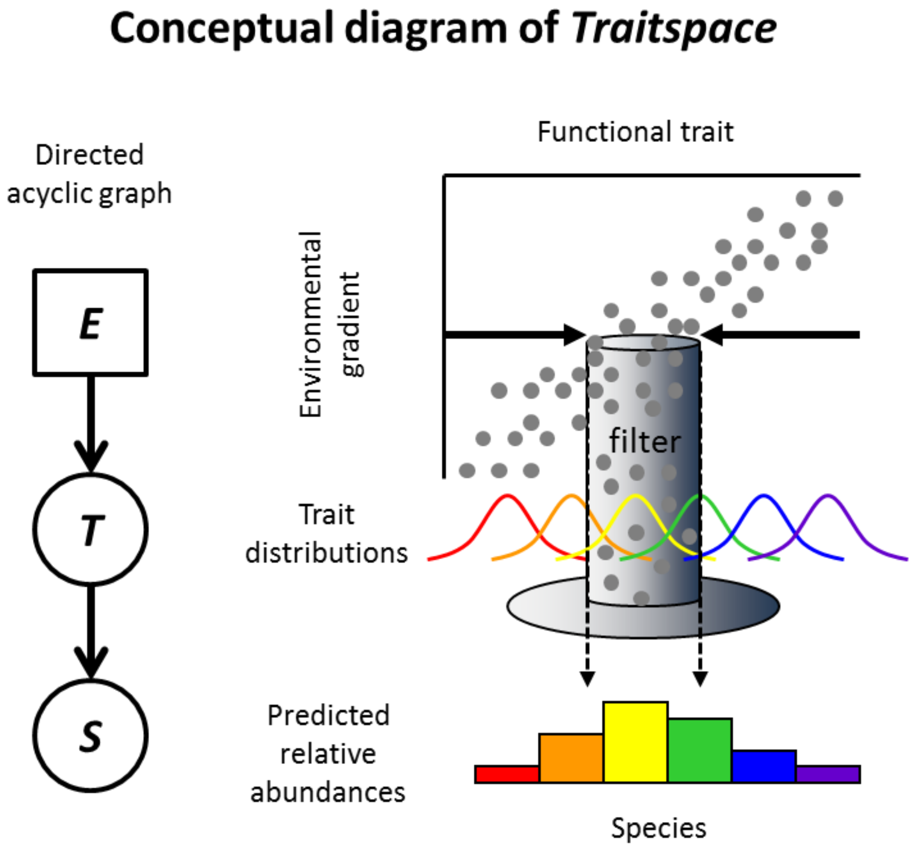


Fig. 1. Conceptual illustration of the Traitspace model illustrating the directed acyclic graph on the left (*E* = environmental gradients, *T* = traits, *S* = species), and trait selection through environmental filters on the right. Grey dots represent hypothetical observed individual-level functional trait values, and the size of the environmental filter (indicated by the arrows at a specific point on the gradient) determines the range of trait values in a given environment. The trait distributions of six hypothetical species indicate that the yellow and green species should be the most likely to occur in that environment because their trait values occur within the range of the filter. Reproduced from Laughlin et al. (2012).

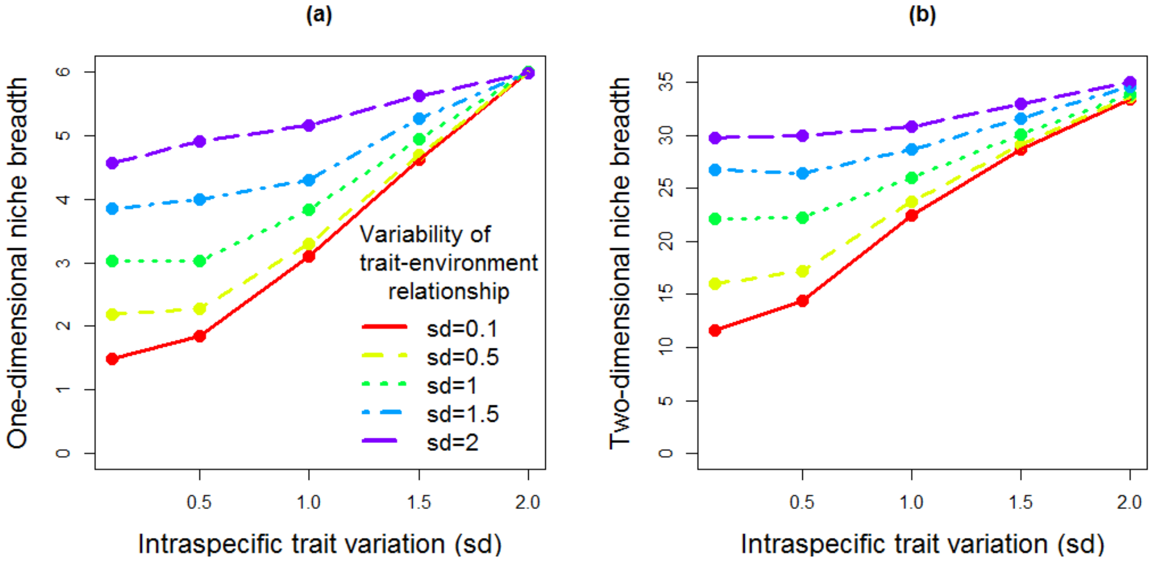


Fig. 2. Niche breadth decreases as intraspecific trait variation decreases and as the strength of the environmental filter increases. These results came from simulations of the model where relative abundances were predicted using one trait and either (a) one or (b) two environmental gradients, and niche breadths shown here correspond only to the species that reached peak abundance in the middle of the gradient to avoid truncated distributions. Niche breadth was calculated as the length or area within the environmental space where predicted relative abundances > 0.05.

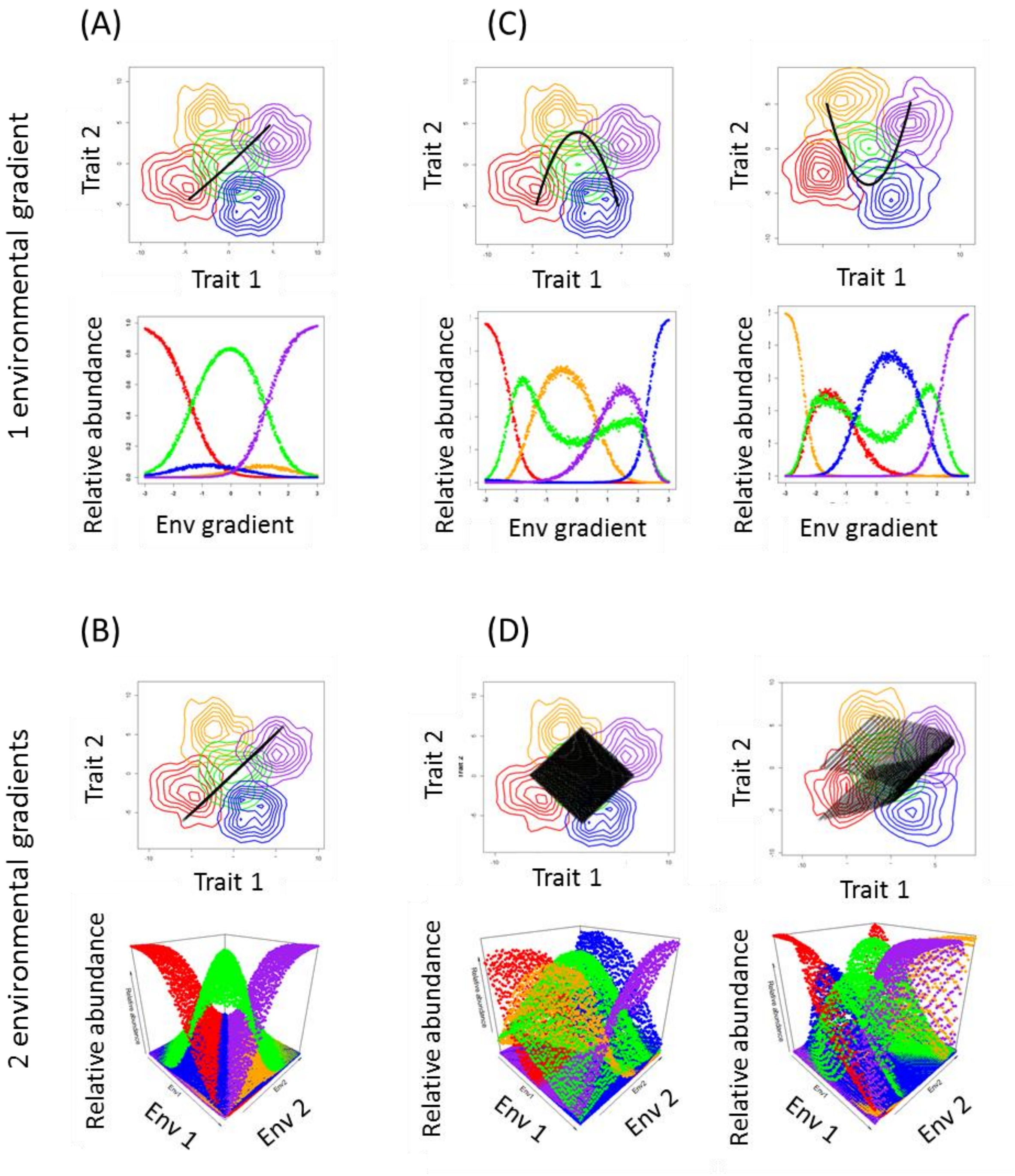


Fig. 3. Species will not occupy an environmental niche if their trait values do not promote fitness in any environmental condition. The black lines or regions illustrated within these two-dimensional trait spaces illustrate the model-fitted trait values from the trait-environment regression models, and the Traitspace predictions following from these model-fitted trait values are illustrated immediately below the 2-dimensional trait spaces. (A and B) If the

black lines or regions only overlap some species (red, green, and purple species), then the other species (orange and blue species) will be selected against and will not occupy a niche. (C) In the case of a single environmental gradient, non-linear trait-environment relationships are necessary for all species to occupy an environmental niche. (D) In the case of two environmental gradients, there are generally far more possible trait combinations that can promote fitness, and therefore more species will occupy environmental niches.

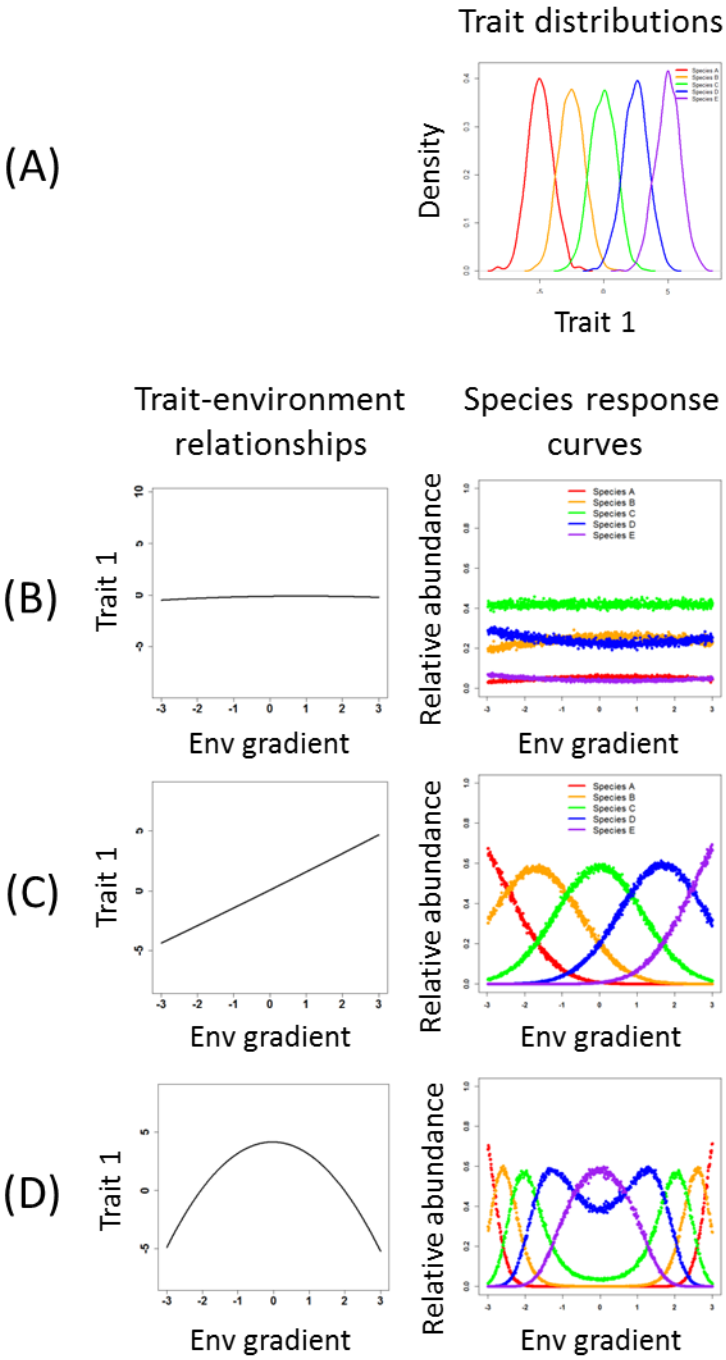


Fig. 4. Model results for one trait and one environmental gradient using three contrasting trait-environment relationships. (A) Trait distributions for 5 species that are evenly spaced within trait space. (B-D) Predicted species response curves when the trait-environment relationships are (B) flat, i.e. neutral, (C) positive linear, and (D) nonlinear hump-shaped.

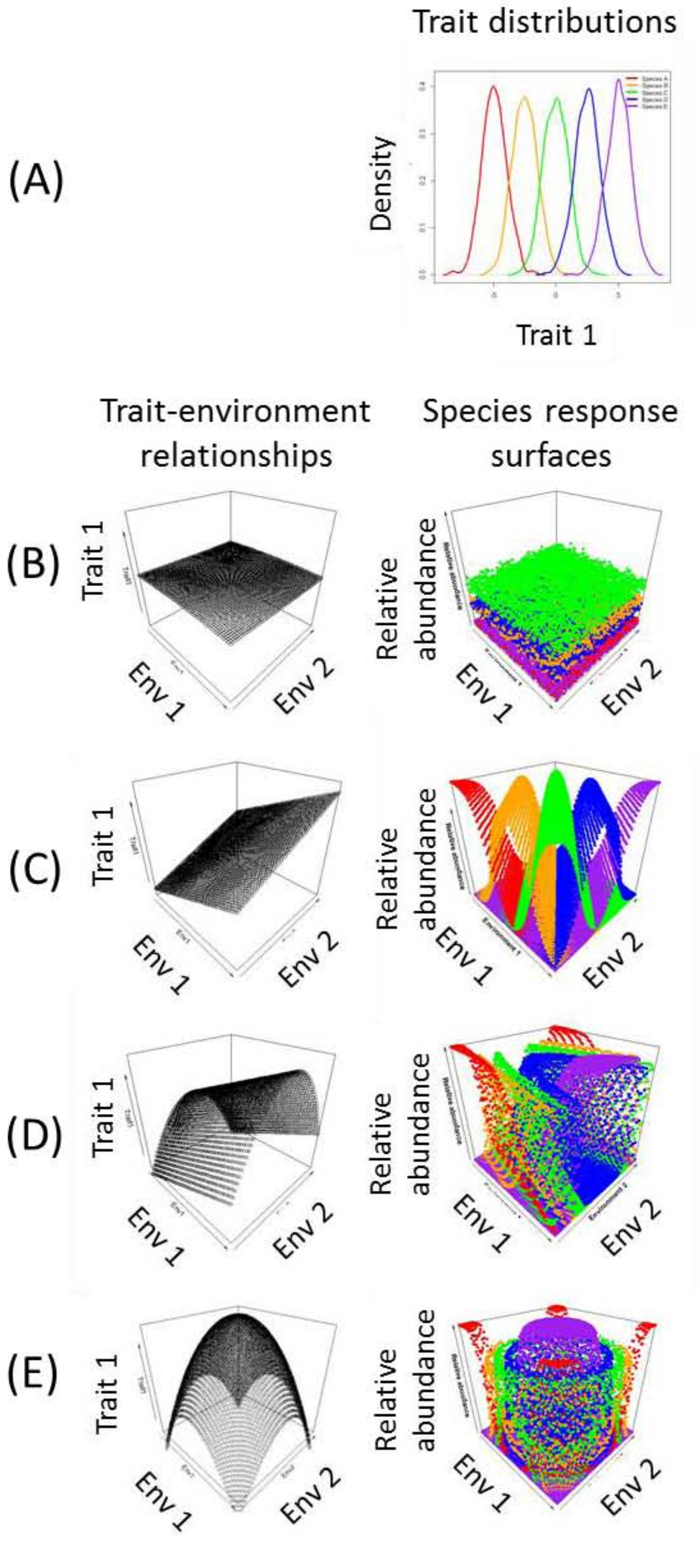
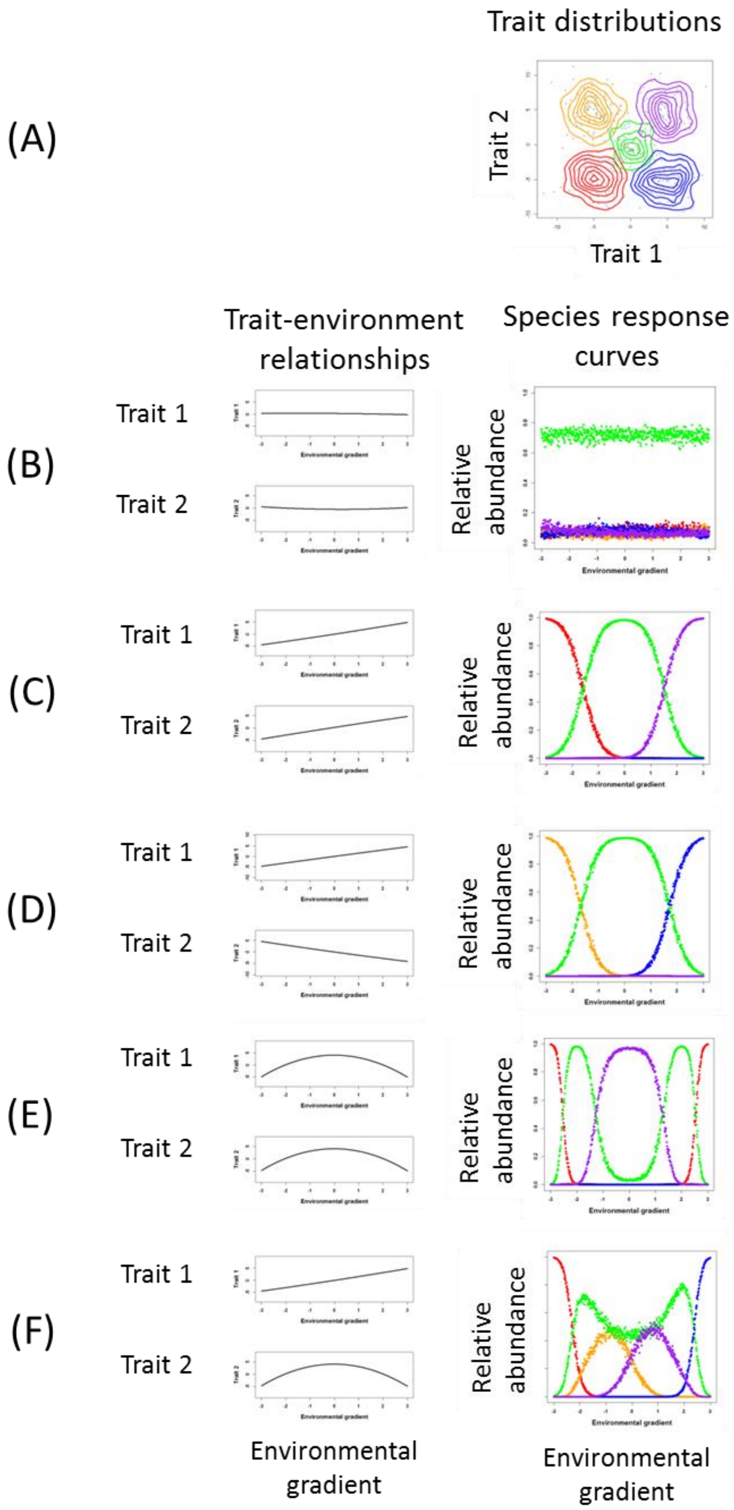


Fig. 5. Model results for one trait and two environmental gradients using four contrasting trait-environment relationships. (A) Trait distributions of species that are evenly spaced within trait space. (B-E) Predicted species response surfaces when (B) the trait is not related

to either environmental gradient, (C) the trait is positively linearly related to both environmental gradients, (D) the trait is positively linearly related to one gradient and exhibits a nonlinear hump-shaped relationship with the second gradient, and (E) the trait exhibits a nonlinear hump-shaped relationship to both gradients.



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656 **Fig. 6**. Model results for two traits and one environmental gradient using five contrasting trait-environment relationships. (A) Bivariate trait distributions for species that are evenly spaced within trait space. (B-F) Predicted species response curves when (B) neither trait is related to the environmental gradient, (C) both traits are positively linearly related to the

environmental gradient, (D) one trait is positively linearly related to the gradient and the other trait is negatively linearly related to the gradient, (E) both traits exhibit nonlinear hump-shaped relationships to the gradient, and (F) one trait exhibits a positive linear relationship with the gradient and the other trait exhibits a nonlinear hump-shaped relationship to the gradient.

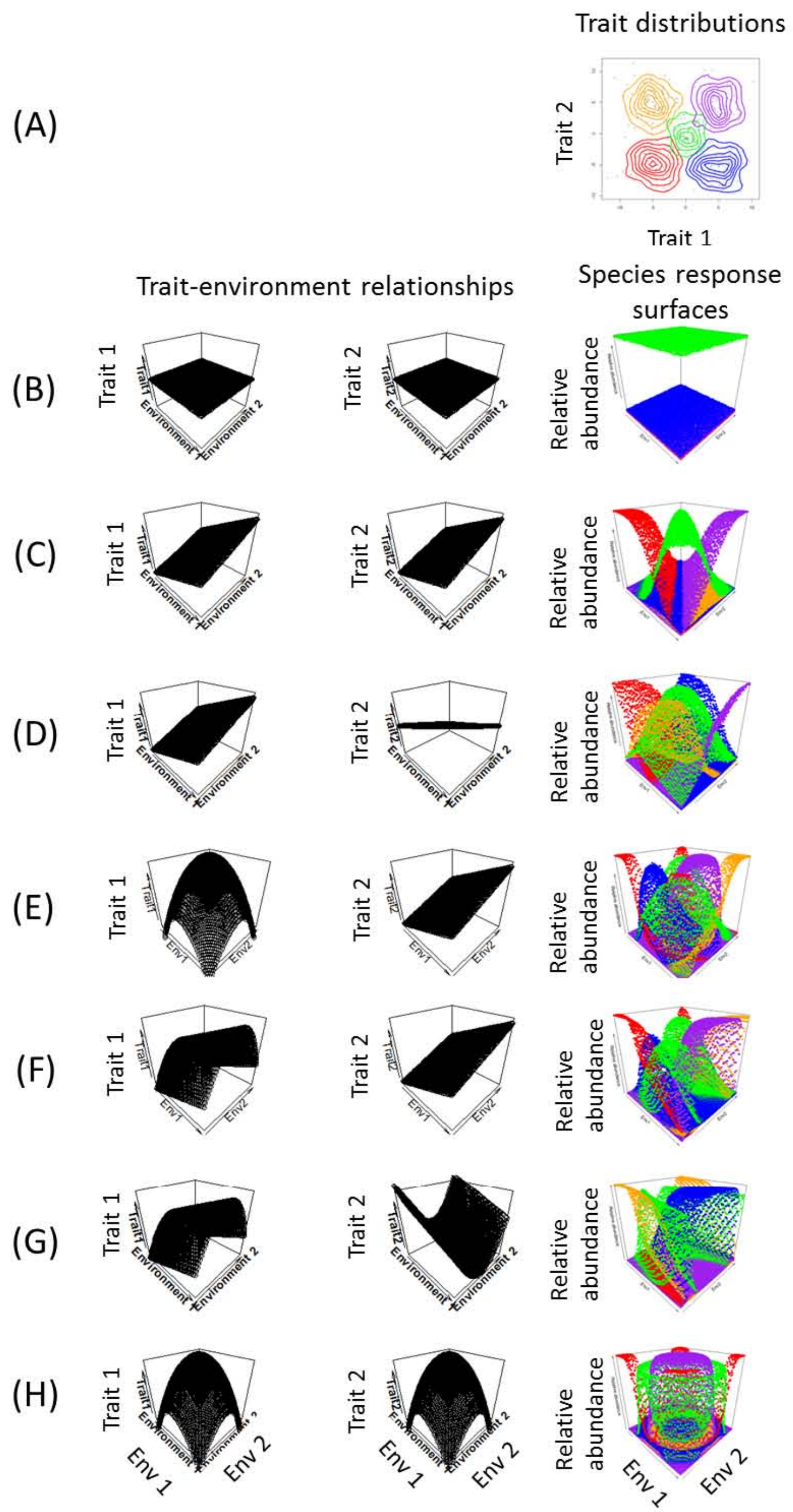

Fig. 7. Model results for two traits and two environmental gradients using seven contrasting trait-environment relationships. (A) Bivariate trait distributions for species that are evenly

spaced within trait space. (B-H) Predicted species response surfaces when (B) neither trait is related to either environmental gradient, (C) both traits are positively linearly related to both environmental gradients, (D) one trait is positively linearly related to both gradients and the other trait is positively linearly related to one gradient while being negatively linearly related to the other gradient, (E) one trait exhibits a nonlinear hump-shaped relationship to both gradients and the other trait is positively linearly related to both gradients, (F) one trait is positively related to one gradient but exhibits a nonlinear hump-shaped relationship to the other gradient and the other trait is positively linearly related to both gradients, (G) one trait is positively related to one gradient but exhibits a nonlinear hump-shaped relationship to the other gradient and the other trait is negatively linearly related to one gradient but exhibits a nonlinear u-shaped relationship with the other gradient, and (H) both traits exhibits nonlinear hump-shaped relationships to both gradients.